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Harpacticoida (Crustacea: Copepoda) associated with cold-water coral substrates in the Porcupine Seabight (NE Atlantic): species composition, diversity and reflections on the origin of the fauna

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SUMMARY: The harpacticoid copepod fauna associated with the coral degradation zone of *Lophelia pertusa* (Linnaeus, 1758) reefs was investigated for the first time in the Porcupine Seabight (NE Atlantic). The species list of the coral degradation zone includes 157 species, 62 genera and 19 families, and the most species-rich families were Ectinosomatidae (36 species), Ameiridae (29 species) and Argostidae (17 species). At least 80% of the species were considered new to science. Most of the 23 known species have been reported from NE Atlantic coastlines and from higher latitudes in northern Subpolar and Polar Seas. At the family level, the harpacticoid fauna in the Porcupine Seabight did not seem to differ markedly from other deep-sea areas, with essentially the same abundant families. However, the presence of typically epifaunal taxa indicates that the hard substrates of the coral degradation zone provide an exceptional habitat. Further, harpacticoid composition and diversity of sediment and coral fragments were compared with similar substrates in a tropical reef lagoon (Zanzibar, Tanzania). Both regions harboured different fauna and the difference between coral and sediment was more obvious in the tropical lagoon. Species richness and evenness of the two microhabitats in the tropical lagoon were lower than in the deep sea.

Keywords: cold-water corals, harpacticoid copepods, species composition, north-east Atlantic, Porcupine Seabight.

RESUMEN: HARPACTICOÍDEOS (CRUSTACEA: COPEPODA) ASOCIADOS A SUSTRATOS DE CORALES DE AGUAS FRÍAS EN PORCUPINE SEABIGHT (NE ATLÁNTICO): COMPOSICIÓN ESPECÍFICA, DIVERSIDAD Y REFLEXIONES SOBRE EL ORIGEN DE LA FAUNA. – Por primera vez, se ha investigado la fauna de copépodos harpacticoídeos asociada a la zona de degradación del coral de arrecifes de *Lophelia pertusa* (Linneo, 1758), de Porcupine Seabight (NE Atlántico). El listado de especies de la zona de degradación del coral incluye 157 especies, 62 géneros y 19 familias. Las familias con mayor riqueza de especies fueron Ectinosomatidae (36 especies), Ameiridae (29 especies) y Argostidae (17 especies). En conjunto, al menos el 80% de las especies son consideradas nuevas para la ciencia. La mayoría de las 23 especies conocidas han sido citadas en las costas del NE Atlántico y en altas latitudes del mar Subpolar y Polar. A nivel de familia, la fauna harpacticoídea en Porcupine Seabight no parece ser muy diferente de la de otras áreas de fondos marinos profundos, presentando en esencia las mismas familias dominantes. Sin embargo, la presencia de taxones típicamente epifaúnicos indica que los sustratos duros de la zona de degradación del coral proporcionan un hábitat excepcional. Además, la composición de copépodos harpacticoídeos y la diversidad de sedimento y fragmentos de coral muerto fueron comparados con sustratos similares en una laguna de arrecife tropical (Zanzíbar, Tanzania). Ambas regiones dan abrigo a fauna diferente, y la diferencia entre coral y sedimento fue más evidente en la laguna tropical. La riqueza específica y la equidad de ambos microhábitats en la laguna tropical fueron menores que en fondos marinos profundos.

Palabras clave: corales de aguas frías, copépodos harpacticoídeos, composición específica, NE Atlántico, Porcupine Seabight.

INTRODUCTION

Cold-water corals occur in the upper part of the bathyal zone throughout the world. *Lophelia pertusa* (Linnaeus, 1758) is most frequently recorded from the continental margin of the NE Atlantic (Rogers, 1999; Freiwald, 2002). Previous studies dealing with the associated fauna on either living or dead *L. pertusa* have mainly focused on macro- and mega-fauna (e.g. Jensen and Frederiksen, 1992; Rogers, 1999). Henry and Roberts (2007) reported that the macrofauna on coral mounds is not locally endemic but typically derived from the regional species pool. However, a characteristic yet facultative reef fauna distinguishes coral mounds from other habitats in the Belgica Mound Province (Porcupine Seabight, NE Atlantic). Raes and Vanreusel (2005, 2006) presented the first study on the associated metazoan meiofauna and nematofauna of a cold-water coral degradation zone in the Porcupine Seabight. They concluded that the dead *L. pertusa* framework and associated substrates enable more taxa to be present and particularly favour harpacticoid copepods, naupliar larvae and polychaetes. The nematofauna associated with the large biogenic substrata is composed of a typical slope, sediment-dwelling, interstitial background community, supplemented with taxa adapted to an epifaunal life strategy. In the underlying sediment, the nematode communities are dominated by typical soft sediment slope taxa (Raes and Vanreusel, 2006).

Although harpacticoid copepods are a diverse and abundant part of the deep-sea meiobenthos, general knowledge on their species composition and distribution is still limited (Seifried, 2004). Even in the NE Atlantic Ocean, which is one of the best studied regions concerning the deep-sea meiobenthos, information on harpacticoid diversity and species composition remains remarkably scarce (Vincx *et al.*, 1994). The present paper provides the first comprehensive study on the harpacticoid copepod fauna associated with dead cold-water coral substrates from the deep sea. We will assess whether a cold-water coral degradation zone in the Porcupine Seabight harbours a distinctive harpacticoid fauna compared to the surrounding soft-bottom deep-sea floor. Furthermore, we will discuss the possible affinities to fauna in other habitats which might be connected to these reefs.

Recently, Raes *et al.* (2008) studied community structure and habitat preferences of two typically

epifaunal nematode families (Epsilonematidae and Draconematidae) in deep temperate (Porcupine Seabight) and shallow tropical (Kenya, Indian Ocean) coral degradation zones. Despite the strong environmental differences of these geographically and bathymetrically separated ecosystems, similar (and in some cases even morphologically identical) species were found, which emphasised the importance of microhabitat type in structuring the nematode community. For the harpacticoid copepod fauna, we will compare the composition in a cold-water coral degradation zone (Porcupine Seabight) with the fauna from similar substrates in a tropical reef lagoon (Zanzibar Island, Indian Ocean) (recently studied by Gheerardyn *et al.* (2008b)) and will assess whether diversities in the two degradation zones are of a similar order of magnitude.

MATERIAL AND METHODS

The material studied in this paper was collected during expeditions RV Belgica 00/16, 01/12 and 03/13 in the Porcupine Seabight (NE Atlantic Ocean), in June 2000, May 2001 and May 2003 respectively. Eight sites were sampled with a round box corer (Netherlands Institute for Sea Research, diameter 32 cm) (Fig. 1, Table 1). Six sampling sites in the coral degradation zone of *Lophelia pertusa* reefs yielded 6 sediment, 6 coral and 2 sponge samples. The material from the coral degradation zone was collected at depths between 880 and 1005 m, with boxes 1, 2, 5 and 6 taken from the flanks of two seabed mounds in the Belgica Mound Province, and boxes 3 and 4 taken between these two mounds. In each case, the surface of the sediment was partly or entirely covered with several dead fragments of the cold-water coral *Lophelia pertusa* and skeletons of the glass sponge *Aphrocallistes bocagei* Schultze, 1886. After collecting the coral fragments and sponge skeletons separately, meiofauna of underlying sediment was sampled with three sediment cores (surface area 10 cm²). The underlying sediment mainly consisted of fine to medium sand and a more or less pronounced silt fraction (median grain size between 8.3 and 194.9 µm), and contained small fragments of both biogenic substrates, as well as some small mollusc shells and echinoid radioles. For samples of coral-free sediments, two boxcorers were taken to the west of the mounds in the Arwen Channel (box 7a and 7b) and two boxcorers to the east of the mounds (box 8a and 8b). Three sediment cores

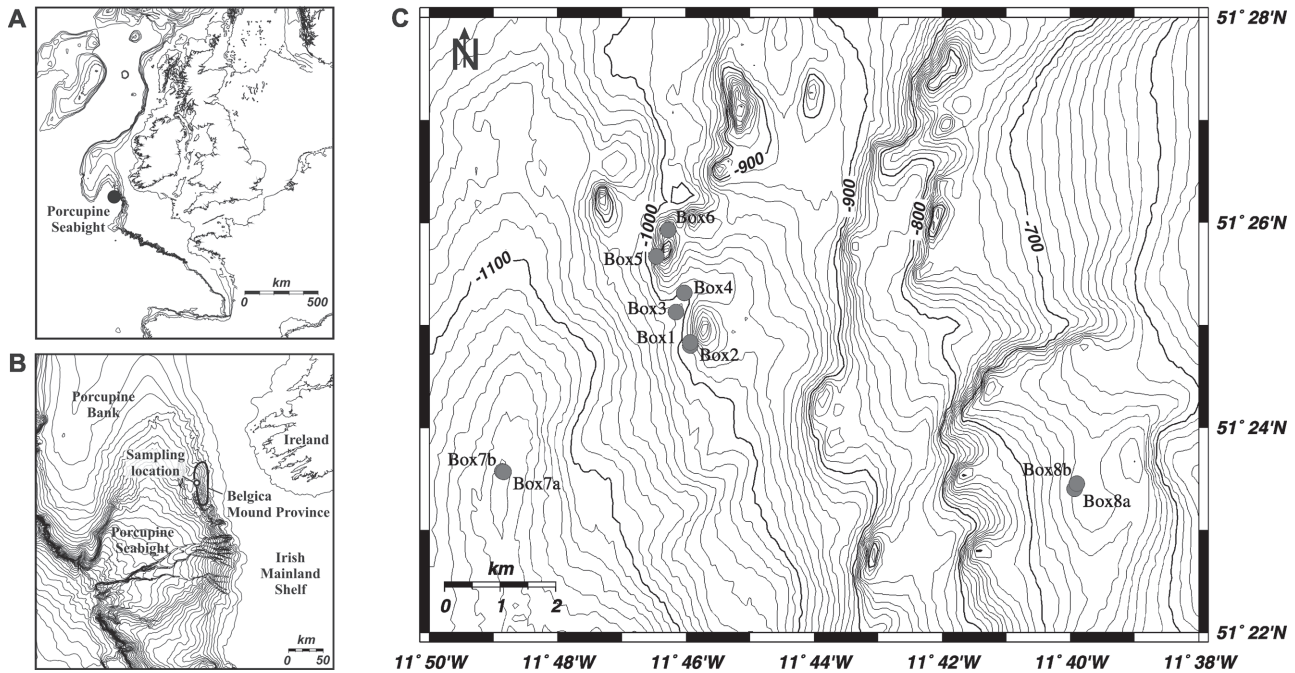


FIG. 1. – (A) Location of the Porcupine Seabight (NE Atlantic Ocean) along the European continental margin, (B) sampling location in the Belgica Mound Province, and (C) a detail showing the ridge of mounds in the Belgica Mound Province, with boxcorers 1-6 taken in the coral degradation zone of two seabed mounds, and boxcorers 7a-b and 8a-b from coral-free sediments (multibeam bathymetry by courtesy of AWI Bremerhaven, contour interval at 10 m).

TABLE 1. – Depth, date, geographical position, and microhabitats sampled per boxcorer taken at the Porcupine Seabight. (sed = underlying sediment, cor = coral fragment, spo = sponge skeleton)

Boxcorer	Date	Coordinates		Depth (m)	Sample
		Latitude	Longitude		
Box1	17.06.2000	51°24.802'N	11°45.924'W	1005	sed, cor, spo
Box2	17.06.2000	51°24.824'N	11°45.932'W	1000	sed, cor
Box3	07.05.2001	51°25.1290'N	11°46.1553'W	972	sed, cor, spo
Box4	07.05.2001	51°25.3120'N	11°46.0226'W	969	sed, cor
Box5	07.05.2001	51°25.6700'N	11°46.4553'W	950	sed, cor
Box6	07.05.2001	51°25.9290'N	11°46.2717'W	880	sed, cor
Box7a	25.05.2003	51°23.572'N	11°48.859'W	1168	sed
Box7b	25.05.2003	51°23.567'N	11°48.843'W	1175	sed
Box8a	25.05.2003	51°23.403'N	11°39.936'W	649	sed
Box8b	25.05.2003	51°23.454'N	11°39.901'W	646	sed

(10 cm²) were collected per boxcorer and copepods were taken from the upper three centimetres. All material was fixed with 4% buffered formaldehyde. At both coral-free sampling sites, the upper first centimetre layer consisted of fine to medium sand with a small silt fraction (median grain size between 153.6 and 189.3 µm). In total, a surface area of 180 cm² of underlying sediment was collected from the coral degradation zone and 120 cm² of sediment from the coral-free sites.

In the laboratory, each coral or sponge sample was rinsed thoroughly over 1 mm and 32 µm sieves to collect macro- and meiofauna respectively. Meiofauna from the sediment was extracted by density gradient centrifugation, using Ludox HS40 (spe-

cific density 1.18) as a flotation medium (Heip *et al.*, 1985). The first 200 randomly encountered copepods per sample (or all copepods when less than 200 were present) were picked out and mounted in glycerine. All adult harpacticoids were identified to species using Lang (1948, 1965), Huys *et al.* (1996), Boxshall and Halsey (2004) and original species descriptions. Assignment of species to genera and families was in accordance with recent literature. The systematic status of Pseudotachidiidae Lang, 1936 and Rhynchothalestridae Lang, 1948 follows Willen (2000), the status of Miraciidae Dana, 1846 follows Willen (2000, 2002), and the status of Idyanthidae Lang, 1944, Neobradyidae Olofsson, 1917 and Zosimidae Seifried, 2003 follows Seifried (2003).

TABLE 2. – List of identified families, genera and species from the Porcupine Seabight. For each species, the number of collected specimens from the coral degradation zone is given (between parentheses). Number of collected specimens from coral-free sites 7 and 8 are provided separately (⁷ or ⁸: from coral-free site 7 or 8, respectively).

Family Ameiridae Monard, 1927	
<i>Ameira</i> Boeck, 1865:	sp. 1 (37), sp. 2 (2), sp. 3 (28; 1 ⁷), sp. 4 (1), sp. 5 (1), sp. 6 (1 ⁸)
<i>Ameiropsis</i> Sars, 1907:	sp. 1 (3), sp. 2 (2), sp. 3 (3), sp. 4 (2), sp. 5 (2), sp. 6 (1)
<i>Filexilia</i> Conroy-Dalton and Huys, 1997:	sp. 1 (3)
<i>Leptomesochra</i> Sars, 1911:	sp. 1 (16), sp. 2 (2)
<i>Malacopsyllus</i> Sars, 1911:	new sp. 1 (4), new sp. 2 (1)
<i>Parapseudoleptomesochra</i> Lang, 1965:	sp. 1 (3), sp. 2 (9)
<i>Pseudameira</i> Sars, 1911:	sp. 1 (1), sp. 2 (8; 1 ⁷)
<i>Sarsameira</i> Wilson, 1924:	sp. 1 (16), sp. 2 (4)
<i>Stenocopia</i> Sars, 1907:	new sp. 1 (4), new sp. 2 (9), new sp. 3 (1)
Ameirinae Lang, 1944 unidentified:	sp. 1 (1), sp. 2 (1), sp. 3 (1), sp. 4 (1)
Family Ancorabolidae Sars, 1909	
<i>Ancorabolina</i> George, 2006:	<i>A. belgicae</i> Gheerardyn and George, in press (1)
<i>Laophontodes</i> T. Scott, 1894:	<i>L. mourois</i> Arroyo, George, Benito and Maldonado, 2003 (5)
<i>Lobopleura</i> Conroy-Dalton, 2004:	<i>L. expansa</i> (Sars, 1908) (3)
Family Argestidae Por, 1986	
<i>Argestes</i> Sars, 1910:	new sp. 1 (5), new sp. 2 (2), new sp. 3 (2), new sp. 4 (1), new sp. 5 (1)
<i>Bodinia</i> George, 2004:	new sp. 1 (7)
<i>Dizahavia</i> Por, 1979:	new sp. 1 (9)
<i>Eurycletodes</i> Sars, 1909:	<i>E. (O.) cf. similis</i> (T. Scott, 1895) (7), new sp. 1 (1 ⁷), new sp. 2 (1)
<i>Fultonina</i> T. Scott, 1902:	<i>F. cf. bougisi</i> Soyer, 1964 (12), new sp. 1 (11)
<i>Mesocletodes</i> Sars, 1909:	<i>M. guillei</i> Soyer, 1964 (1), <i>M. irrasus</i> (T. and A. Scott, 1894) (1), new sp. 1 (1), new sp. 2 (2), new sp. 3 (2)
Argestidae unidentified:	sp. 1 (3)
Family Canthocamptidae Sars, 1906	
<i>Bathycamptus</i> Huys and Thistle, 1889:	new sp. 1 (6), new sp. 2 (2), new sp. 3 (1)
<i>Mesochra</i> Boeck, 1865:	<i>M. pygmaea</i> (Claus, 1863) (9)
Canthocamptidae unidentified:	sp. 1 (1), sp. 2 (3), sp. 3 (2), sp. 4 (4), sp. 5 (6), sp. 6 (5), sp. 7 (1), sp. 8 (1), sp. 9 (1 ⁷), sp. 10 (1 ⁸)
Family Cletodidae T. Scott, 1905	
<i>Cletodes</i> Brady, 1872:	sp. 1 (1; 2 ⁸), sp. 2 (1 ⁸), sp. 3 (1 ⁸)
<i>Enhydrosoma</i> Boeck, 1872:	sp. 1 (1)
Family Ectinosomatidae Sars, 1903	
<i>Bradya</i> Boeck, 1873:	new sp. 1 (1), new sp. 2 (2)
<i>Bradyellopsis</i> Brian, 1924:	new sp. 1 (1)
<i>Ectinosoma</i> Boeck, 1865:	new sp. 1 (9), new sp. 2 (3), new sp. 3 (1 ⁸), new sp. 4 (3)
<i>Halectinosoma</i> Lang, 1944:	new sp. 1 (1), new sp. 2 (1 ⁸), new sp. 3 (1)
<i>Halophytophilus</i> Brian, 1919:	<i>H. lopheliae</i> Gheerardyn, Seifried and Vanreusel, 2008 (27; 1 ⁸), new sp. 1 (13), new sp. 2 (4), new sp. 3 (1 ⁷)
<i>Hastigerella</i> Nicholls, 1935:	new sp. 1 (2), new sp. 2 (1 ⁸)
<i>Klieosoma</i> Hicks and Schriever, 1985:	<i>K. triarticulatum</i> (Klie, 1949) (8), new sp. 1 (4), new sp. 2 (4)
<i>Lineosoma</i> Wells, 1965:	new sp. 1 (1), new sp. 2 (1 ⁷)
<i>Microsetella</i> Brady and Robertson, 1873:	<i>M. norvegica</i> (Boeck, 1865) (16)
<i>Parabradia</i> Lang, 1944:	new sp. 1 (1), new sp. 2 (5)
<i>Peltobradia</i> Médioni and Soyer, 1968:	new sp. 1 (1)
<i>Pseudobradia</i> Sars, 1904:	<i>P. cf. banyulensis</i> Soyer, 1974 (38), <i>P. cf. peresi</i> Soyer, 1974 (1), new sp. 1 (2), new sp. 2 (5), new sp. 3 (1), new sp. 4 (2), new sp. 5 (3), new sp. 6 (1 ⁷)
<i>Sigmatidium</i> Giesbrecht, 1881:	<i>S. cf. parvulum</i> Mielke, 1974 (1), <i>S. cf. triarticulatum</i> Mielke, 1979 (3), new sp. 1 (7), new sp. 2 (4), new sp. 3 (2), new sp. 4 (12), new sp. 5 (45), new sp. 6 (1 ⁷)
Ectinosomatidae unidentified:	new sp. 1 (1), new sp. 2 (1)
Family Harpacticidae Sars, 1904	
<i>Perissoscope</i> Brady, 1910:	new sp. 1 (27)
Family Hunttemanniidae Por, 1986	
<i>Metahunttemannia</i> Smirnov, 1946:	new sp. 1 (1), new sp. 2 (1; 1 ⁷)
<i>Talpina</i> Dahms and Pottek, 1992:	new sp. 1 (1 ⁷)
Family Idyanthidae Lang, 1944	
<i>Idyanthe</i> Sars, 1909:	<i>I. dilatata</i> (Sars, 1905) (5), new sp. 1 (3), new sp. 2 (7), new sp. 3 (2), new sp. 4 (1)
<i>Idyella</i> Sars, 1906:	<i>I. major</i> Sars, 1920 (1), new sp. 1 (1)
<i>Nematovorax</i> Bröhlidick, 2005:	<i>N. gebkelinae</i> Bröhlidick, 2005 (1)
Idyanthidae unidentified:	new sp. 1 (3), new sp. 2 (1)
Family Laophontidae T. Scott, 1905	
<i>Archosola</i> Huys and Lee, 2000:	new sp. 1 (1)
<i>Heterolaophonte</i> Lang, 1944:	new sp. 1 (1)
<i>Laophonte</i> Philippi, 1840:	<i>L. elongata</i> Boeck, 1872 (5), new sp. 1 (14), new sp. 2 (2), new sp. 3 (7)
Family Miraciidae Dana, 1846	
<i>Amphiascus</i> Sars, 1905:	sp. 1 (26 ; 2 ⁸), sp. 2 (7), sp. 3 (1 ⁸)
<i>Amphiascoides</i> Nicholls, 1941:	sp. 1 (6; 2 ⁸)
<i>Haloschizopera</i> Lang, 1944 :	sp. 1 (9 ; 3 ⁷)
<i>Rhyncholagena</i> Lang, 1944:	sp. 1 (11)
<i>Robertgurneya</i> Lang, 1944:	sp. 1 (2 ⁸)

TABLE 2 (cont.). – List of identified families, genera and species from the Porcupine Seabight. For each species, the number of collected specimens from the coral degradation zone is given (between parentheses). Number of collected specimens from coral-free sites 7 and 8 are provided separately (⁷ or ⁸: from coral-free site 7 or 8, respectively).

Family Neobradziidae Olofsson, 1917	
<i>Marsteinia</i> Drzycimski, 1968:	new sp. 1 (5), new sp. 2 (1), new sp. 3 (3)
Neobradziidae unidentified:	new sp. 1 (6)
Family Normannellidae Lang, 1944	
<i>Sagamiella</i> Lee and Huys, 1999:	new sp. 1 (2 ⁸)
Family Novocriniidae Huys and Iliffe, 1998	
<i>Atergopedia</i> Martínez Arbizu and Moura, 1998:	<i>A. vetusta</i> Martínez Arbizu and Moura, 1998 (3), new sp. 1 (1)
Family Paramesochridae Lang, 1944	
<i>Diarthrodella</i> Klie, 1949:	<i>D. cf. orbiculata</i> Klie, 1949 (1)
<i>Kliopsyllus</i> Kunz, 1962:	new sp. 1 (1 ⁷), new sp. 2 (1 ⁸)
<i>Leptopsyllus</i> T. Scott, 1894:	new sp. 1 (6), new sp. 2 (1 ⁸)
<i>Paramesochra</i> T. Scott, 1892:	new sp. 1 (8), new sp. 2 (3), new sp. 3 (2), new sp. 4 (2; 1 ⁷), new sp. 5 (1 ⁷)
<i>Scottopsyllus</i> Kunz, 1962:	<i>S. (Sc.) cf. robertsoni</i> (T. and A. Scott, 1895) (1)
Paramesochridae unidentified:	sp. 1 (1 ⁷)
Family Pseudotachidiidae Lang, 1936	
<i>Cylindronannopus</i> Coull, 1973:	new sp. 1 (2)
<i>Idomene</i> (?) Philippi, 1843:	sp. 1 (2), sp. 2 (5)
<i>Pseudomesochra</i> T. Scott, 1902:	new sp. 1 (31), new sp. 2 (8), new sp. 3 (6), new sp. 4 (45), new sp. 5 (11), new sp. 6 (3), new sp. 7 (3)
<i>Xylora</i> Hicks, 1988:	new sp. 1 (2), new sp. 2 (10)
Pseudotachidiidae unidentified:	sp. 1 (2)
Family Rhynchothalestridae Lang, 1948	
<i>Rhynchothalestris</i> Sars, 1905:	new sp. 1 (7)
Family Tegastidae Sars, 1904	
<i>Tegastes</i> Norman, 1903:	sp. 1 (1)
Family Tetragonicipitidae Lang, 1944	
Tetragonicipitidae new gen. 1:	new sp. 1 (6)
Family Zosimidae Seifried, 2003	
<i>Zosime</i> Boeck, 1872:	<i>Z. bergensis</i> Drzycimski, 1968 (4; 1 ⁸), <i>Z. paramajor</i> Bodin, 1968 (1), <i>Z. pacifica</i> Fiers, 1991 (1 ⁸), new sp. 1 (1 ⁷)
Harpacticoida incertae sedis	
<i>Parameiopsis</i> Becker, 1974:	<i>P. antennafortis</i> Corgosinho and Gheerardyn, 2009 (1)
Unidentified sp. 1 (1)	
Unidentified sp. 2 (2)	

Rarefaction curves (Sanders, 1968), calculated using the methods of Hurlbert (1971), were used to compare species richness. Equitability of the copepod fauna was studied based on species' abundance distributions as k-dominance curves (Lambshhead *et al.*, 1983). Calculations were done using the PRIMER5 software (Clarke and Gorley, 2001).

Species composition and diversity of dead coral fragments and underlying sediment are compared with similar substrates from a tropical reef lagoon along the eastern coast of Zanzibar Island (Tanzania). Meiofauna samples were collected in August 2004 at two locations, Matemwe (5°52'S, 39°21'E) and Makunduchi (6°25'S, 39°34'E). The distance between the two locations is 70 km and sampling occurred during low tide, under a water cover of 0.5 m. At each location, three replicates were taken at a distance of five metres from each other, at approximately 400-500 m from the beach. For each replicate, a round, metal core (diameter 30 cm) was placed onto the sediment to delimit the sampling area. Within this metal core, meiofauna of coral sand was sampled with one sediment core (surface area 10 cm²). The dead coral fragment was taken out

manually and put directly in a plastic bag. In total, a surface area of 60 cm² of coral sand was collected from the tropical reef lagoon. Further processing of the samples and laboratory analyses are described in Gheerardyn *et al.* (2008b).

RESULTS

In total, 901 adult harpacticoids were analysed from the Porcupine Seabight (860 from the coral degradation zone, 18 from coral-free sediments at site 7 and 23 from coral-free sediments at site 8) and this yielded 181 species (Table 2), two of which could not be assigned to any family and were treated as Harpacticoida incertae sedis. The remaining 179 species were spread over 20 families. At present, 22 species cannot be assigned unequivocally to a known genus and are assigned to their respective suprageneric taxon (e.g. subfamily Ameirinae). The other 157 species were spread over 66 genera, with one genus being new in Tetragonicipitidae. Due to the high number of species, it was necessary to restrict the processing and therefore 54 species

TABLE 3. – Distribution of currently described species found in the Porcupine Seabight (NE Atlantic).

Species	Location	Habitat	Microhabitat	Reference
<i>Ancorabolina belgicae</i>	Porcupine Seabight (NE Atlantic)	cold-water coral degradation zone, depth of 880 m	fine to medium sand	Gheerardyn and George (in press)
<i>Atergopodia vetusta</i>	continental slope NW off Franz Josef Land (Barents Sea, Arctic Ocean)	depth of 534 m	muddy sediments covered by mat of sponges spicula about 2 cm thick	Martínez Arbizu and Moura (1998)
<i>Diarthrodella cf. orbiculata</i>	Helgoland (Germany, North Sea)		shelly sediments	Klie (1949)
<i>Eurycletodes (O.) cf. similis</i>	Roscoff (France, Atlantic Ocean)		sand	Bocquet and Bozic (1955)
	Franz Josef Land, Spitsbergen, König-Oscar Land, Lofoten, South coast of Norway, Sweden, Scotland, England, Ireland, France (Roscoff)	different depths (to 108 m), eurytope	Sweden: between red algae, on 'Lophahelia-Riff', and on hard bottom at 200 m depth	several authors in Lang (1948)
	Cape of Sorrento (Italy, Mediterranean Sea)	submarine cave in littoral	beneath <i>Balanus perforatus</i> sponges	Pesta (1959)
<i>Fultonia cf. bougisi</i>	Franz Josef Land			Chislenko (1977)
	Atlantic, Northern Subpolar Seas, North Sea			George (2004)
	Banyuls-sur-mer (France, Mediterranean Sea)	depth of 360 m, 390 m and 610 m	mud	Soyer (1964a)
	Banyuls-sur-mer (France, Mediterranean Sea)	depth of 35 m	biocenose coralligène	Soyer (1966)
	Magellan Region	depth of 101 and 219 m		George (1999)
<i>Halophytophilus lopheliae</i>	Porcupine Seabight (NE Atlantic)	cold-water coral degradation zone and coral-free sediments, depth of 646–1005 m	dead coral fragments, fine to medium sand	Gheerardyn <i>et al.</i> (2008a)
<i>Idyanthe dilatata</i>	west of Norway, polar island north of Grinnell Land	depths ranging from 18 to 54 m		several authors in Lang (1948)
	Karelian coast of the White Sea			Chislenko (1967)
<i>Idyella major</i>	Longyearbyen (Spitzbergen)	intertidal zone		Mielke (1974)
	Christiansand (Norway)	depth of 54 m		Sars (1920)
	Gullmar Fjord (Sweden)	depth of 30–70 m	mud	Lang (1948)
<i>Klieosoma triarticulatum</i>	Helgoland (Germany, North Sea)	tidal pool	sand	Klie (1949)
	Helgoland (Germany, North Sea)		on <i>Laminaria</i>	Hicks and Schriever (1985)
<i>Laophonte elongata</i>	NE Atlantic (Norway, Sweden, Ireland, Roscoff), Mediterranean Sea (Banyuls, Algier, Venice)	to a depth of 45 m	mud, sand, on <i>Posidonia</i> , between algae	several authors in Lang (1948)
	Tenerife (Canary Islands)	exposed beach	coarse sand to cobbles	Noodt (1958)
	Cape of Sorrento (Italy, Mediterranean Sea)	submarine cave in littoral		Pesta (1959)
	NW coast of Black Sea	littoral		Por (1960)
	Bergen (Norway)	depth of 512 m		Drzyckiński (1969)
	Santa Cruz, Argentina (South Atlantic)	infralittoral	between <i>Macrocystis</i>	Pallares (1970)
	Bulgary (Black Sea)			Marinov (1971)
	Crimea (Black Sea)			Apostolov (1972)

	France (Mediterranean Sea)			Kunz (1975)
	Bulgary (Black Sea)			Apostolov and Marinov (1988)
	numerous localities along NE Atlantic shores and Mediterranean Sea	depths to 260 m	sediments, maerl, washings of crabs, dead corals and algae	Fiers (1988)
	Concepción (Chile)		washings of several decapods	Fiers (1988)
	west coast of Florida (U.S.A.)	depth 36 to 40 m	washings of 2 specimens of <i>Pilumnus sayi</i>	Fiers (1988)
<i>Laophontodes mourois</i>	Island of Mouro (northern coast of Spain)	depth of 12 m	holdfasts of <i>Laminaria ochroleuca</i>	Arroyo <i>et al.</i> (2003)
<i>Lobopleura expansa</i>	Saltenfjord (Norway)			Sars (1908), Conroy-Dalton (2004)
<i>Mesochra pygmaea</i>	numerous localities along NE and NW Atlantic shores, Mediterranean Sea, Black Sea	large vertical distribution (littoral to depth of 286 m)	between algae, on sandy and muddy bottom	several authors in Lang (1948)
	Angola (South Atlantic Ocean)	littoral		Candeias (1959)
	Karelian coast of the White Sea			Chislenko (1967)
	numerous localities all over the world (e.g. Arctic waters, eastern coast North America, Mozambique, southern Australia)			Hamond (1971)
<i>Mesocletodes guillei</i>	Banyuls-sur-mer (France, Mediterranean Sea)	depth of more than 50 m		Soyer (1964b)
<i>Mesocletodes irrasus</i>	South coast of Norway, Sweden, Scotland	depth of 30-145 m	muddy bottom	several authors in Lang (1948)
	Banyuls-sur-mer (France, Mediterranean Sea)	depth of 390 m		Soyer (1964b)
	Atlantic, Northern Subpolar Seas, Mediterranean Sea			George (2004)
<i>Microsetella norvegica</i>	widely distributed in all oceans			several authors in Lang (1948)
<i>Nematovorax gebkelinae</i>	Angola Basin (South Atlantic Ocean)	depth of 5389-5450 m	mud	Bröhlidick (2005)
<i>Parameiropsis antennaeformis</i>	Porcupine Seabight (NE Atlantic)	cold-water coral degradation zone, depth of 880 m	fine to medium sand	Corgosinho and Gheerardyn (2009)
<i>Pseudobradia cf. banyulensis</i>	Banyuls-sur-mer (France, Mediterranean Sea)	depth of 32-91 m	mud	Soyer (1974)
<i>Pseudobradia cf. peresi</i>	Banyuls-sur-mer (France, Mediterranean Sea)	depth of 104-108 m	sables du large	Soyer (1974)
<i>Scottopsyllus cf. roberisoni</i>	Firth of Forth, Scotland (North Sea)	tidal pools		Lang (1948)
	Nessebar, Bulgary (Black Sea)			Apostolov (1972)
	Bulgary (Black Sea)			Apostolov and Marinov (1988)
<i>Sigmatidium cf. parvulum</i>	Longyearbyen (Spitzbergen)	intertidal zone		Mielke (1974)
<i>Sigmatidium cf. triarticulatum</i>	Galapagos Islands (Pacific Ocean)	sandy beach		Mielke (1979)
<i>Zosime bergensis</i>	west coast of Norway	fjords and coastal waters, depth of 105-680 m	sandy and muddy bottom	Drzycimski (1968)
<i>Zosime paramajor</i>	Bay of Biscay (Atlantic Ocean)	depth of 900 m	mud	Bodin (1968)
	off North Carolina (NW Atlantic)	depth>1000 m		Coull (1973)
<i>Zosime pacifica</i>	Santa Maria Basin, California (Pacific Ocean)	depth of 50-565 m		Fiers (1991)

within Ameirinae, Canthocamptidae, Cletodidae and Miraciidae were determined to morphospecies-level. However, 127 species were carefully checked against original species descriptions and, of these, 104 species (or 81.9%) were new to science. The identification of certain species (8 of the 23 known) has to be considered with some reservations (specific names indicated with cf.). Until now, three of the new species (*Halophytophilus lopheliae* Gheerardyn, Seifried and Vanreusel, 2008; *Parameiropsis antennofortis* Corgosinho and Gheerardyn, 2009; *Ancorabolina belgicae* Gheerardyn and George, in press) have been described (Gheerardyn *et al.*, 2008a; Corgosinho and Gheerardyn, 2009; Gheerardyn and George, in press) and one species (*Atergopedia* nov. sp. 1) is currently under description.

The samples of the coral degradation zone yielded 157 species belonging to 62 genera and 19 families. In the coral degradation zone, Ectinosomatidae, Ameiridae and Argostidae were the most species-rich families with 36, 29 and 17 species respectively. Pseudotachidiidae, Canthocamptidae and Idyanthidae were represented by 13, 12 and 10 species respectively. The following families were represented by between seven and two species each (in order of decreasing number of species): Paramesochridae, Laophontidae, Miraciidae, Neobradyidae, Ancorabolidae, Cletodidae, Zosimidae, Huntmanniidae and Novocriniidae. The remaining four families (Harpacticidae, Rhynchothalestridae, Tegastidae and Tetragnathidae) were monospecific. The most species-rich genera were *Pseudobradia*, *Pseudomesochra* and *Sigmatidium* (each 7 spp.), and *Ameiropsis* (6 spp.).

The samples from the two coral-free sites added 24 species, 4 genera and 1 family to the complete species list of the Porcupine Seabight. 16 species were collected from site 7 and 18 species from site 8. Each site shared five species with the coral degradation zone. None of the species was present at the two coral-free sites.

Distribution of currently described species found in the Porcupine Seabight

A list of all identified species and data on their geographical and bathymetrical distribution is presented in Table 3. Most of the species (19) have been reported from localities along NE Atlantic coastlines and from higher latitudes in the northern Subpolar and Polar Seas. *Laophonte elongata* shows a much

wider distribution throughout the Atlantic Ocean, including the Mediterranean Sea, the Black Sea and the Chilean Pacific coast. Furthermore, two of these species have also been found in the Mediterranean Sea (*Eurycletodes similis* and *Mesocletodes irrasus*), one in the Black Sea (*Scottopsyllus robertsoni*) and one in the deep NW Atlantic (*Zosime paramajor*). Up to now, three species were restricted to the Mediterranean Sea (*Mesocletodes guillei*, *Pseudobradia banyulensis* and *P. peresi*), while *Fultonia bougisi* showed a disjunct distribution with reports from the Mediterranean Sea and the Magellan region. Two species can be considered as cosmopolitan species (*Mesochra pygmaea* and *Microsetella norvegica*). Until now, 12 species (including four identified with reservations) were known from their type-locality only, with *Nematorax gebkelinae* (from Angola Basin) and *Zosime pacifica* (from California, Pacific Ocean) the most remarkable in view of the remote location in which they were found.

Certain species (such as *Fultonia bougisi*, *Laophonte elongata*, *Mesochra pygmaea*, *Mesocletodes irrasus*, *Zosime bergensis* and *Z. pacifica*) show a large vertical distribution (eurybathyal) and seem to be capable of penetrating into deeper, bathyal waters. Six species (*Ancorabolina belgicae*, *Atergopedia vetusta*, *Halophytophilus lopheliae*, *Nematorax gebkelinae*, *Parameiropsis antennofortis*, *Zosime paramajor*) are exclusive deep-sea species (so far only occurring below 200 m depth), while all other species have been mostly reported from littoral-sublittoral areas. It is interesting to note that Lang (1948) reported *Eurycletodes similis* from the 'Lophahelia-Riff' (probably a misspelling of *Lophohelia*, synonym of *Lophelia*) near Bohuslän (west coast of Sweden). In addition, Fiers (1988) found *Laophonte elongata* from washings of dead corals collected at a depth of 240–260 m, north of Shetland in the Atlantic Ocean. Most of the known species have been collected from muddy and sandy bottoms, although certain species (*Klieosoma triarticulatum*, *Laophonte elongata*, *Laophontodes mourois* and *Mesochra pygmaea*) seem to show a preference for phytal environments.

Comparison with the harpacticoid fauna in a tropical reef lagoon

Composition

At the family level, it was clear that both examined regions harboured different faunas and that the

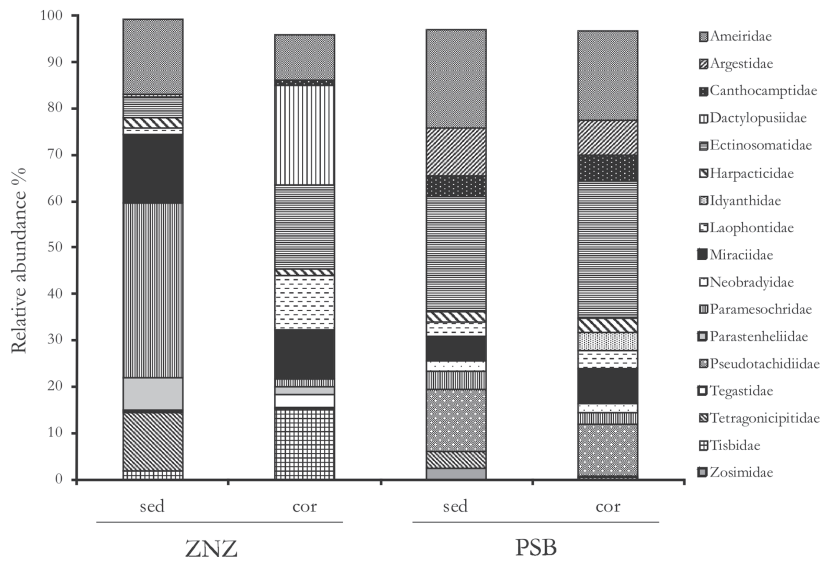


FIG. 2. – Harpacticoid family composition per microhabitat (sed: sediment, cor: coral) in the tropical lagoon on Zanzibar (ZNZ) and the cold-water coral degradation zone at the Porcupine Seabight (PSB), based on pooled samples per microhabitat. Families with a relative abundance >2% in at least one microhabitat (in ZNZ or PSB) are given.

distinction between coral and sediment was clearer in the tropical lagoon (Fig. 2). In total, 29 families were recognised, 13 of which were shared by the two regions. Tropical coral fragments were characterised by high abundance of Dactylopusiidae, Ectinosomatidae, Tisbidae, Laophontidae and Miraciidae (more than 10% of the relative abundance each), while the coral sand was distinguished by the dominance of Paramesochridae, Tetragonicipitidae, Miraciidae and Ameiridae (more than 10% of the relative abundance each). In both microhabitats of the cold-water coral degradation zone, Ameiridae, Argastidae, Ectinosomatidae, Miraciidae and Pseudotachidiidae were the most abundant families (more than 5% of the relative abundance in each of the microhabitats). In total, 101 genera were identified, only 19 of which were shared by the two regions. 47 genera were restricted to the Porcupine Seabight and 35 to the tropical lagoon.

Species diversity

From the tropical substrates (sediment and coral), 1472 adult individuals were analysed, which belonged to 112 species. Although fewer individuals (705) were processed from sediment and coral samples in the Porcupine Seabight, distinctly more species (146) were found. Rarefaction curves of pooled samples per microhabitat in the tropical lagoon at Zanzibar and the deep sea of the Porcupine Seabight indicated a similar trend with a higher diversity

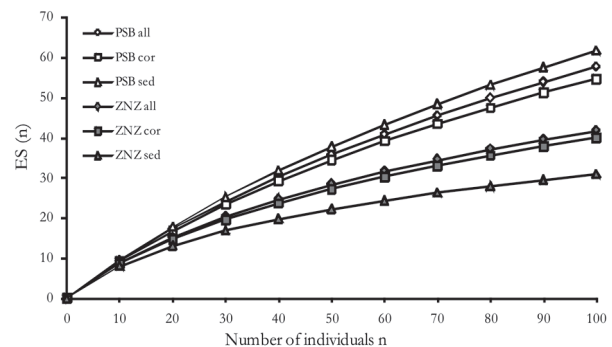


FIG. 3. – Rarefaction curves for pooled samples per microhabitat (sediment: sed, cor: coral) and for the combined community in the two microhabitats (all), in the cold-water coral degradation zone at the Porcupine Seabight (PSB) and the tropical lagoon on Zanzibar (ZNZ). ES (n), expected number of species.

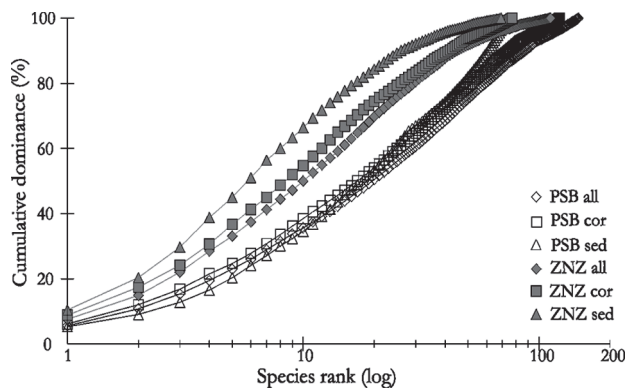


FIG. 4. – K-dominance curves for pooled samples per microhabitat (sediment: sed, cor: coral) and for the combined community in the two microhabitats (all), in the cold-water coral degradation zone at the Porcupine Seabight (PSB) and the tropical lagoon on Zanzibar (ZNZ).

in the Porcupine Seabight (Fig. 3). The expected number of species (ES) for the two coral-free sites ($ES(10) = 9.3$ at site 7; $ES(10)=9.1$ and $ES(20) = 16.2$ at site 8) coincides with rarefaction curves of the cold-water coral degradation zone. Assemblages in the cold-water coral degradation zone showed a more even distribution than in the tropical lagoon, as shown by K-dominance curves (Fig. 4).

DISCUSSION

The present study is the first characterisation of the harpacticoid copepod fauna associated with cold-water coral substrates in the deep sea. Previous meiofauna studies have focused on the composition at a higher taxon level or the nematofauna of *Lophelia pertusa* reef degradation zones in the Belgica Mound Province (Porcupine Seabight, north-east Atlantic) (Raes and Vanreusel, 2005, 2006).

Harpacticoid fauna of the Porcupine Seabight

In the two examined microhabitats (corals and sediment) of the cold-water coral degradation zone, Ameiridae, Argastidae, Ectinosomatidae, Miraciidae and Pseudotachidiidae were the most abundant families. The two coral-free sampling sites yielded too few specimens to compare with the coral degradation zone and assess the influence of coral fragments on species composition and diversity. Therefore, emphasis has been placed on making comparisons with deep-sea studies on soft sediments to assess whether the coral degradation zone harbours a specific fauna. The most abundant families of the coral degradation zone correspond remarkably well to the most abundant of 19 families reported from two abyssal, muddy sites in the Angola Basin, from a water depth of about 5400 m (i.e. Pseudotachidiidae, Argastidae, Ameiridae, Ectinosomatidae and Neobryidae) (Rose *et al.*, 2005). In the present study, the assignment of species to genera and families is in accordance with recent literature as is the case in Rose *et al.* (2005). Vincx *et al.* (1994) reported the assemblages in the deep north-east Atlantic as dominated by Cletodidae, Diosaccidae, Ectinosomatidae, Tisbidae and Cerviniidae. However, at the time, certain genera were assigned to different families. The same caution is recommended when comparing with other studies. Ahnert and Schriever (2001) reported Ameiridae, Ectinosomatidae, Argastidae, Tisbidae

(the majority of the specimens belonging to *Zosime* and *Pseudozosime*, which now belong to Zosimidae) and Neobryidae as the dominant families in the deep sea of the SE Pacific ocean. In Sagami Bay (central Japan, at 1430 m depth), Miraciidae, Ectinosomatidae, Ameiridae and Tisbidae (with species of *Idyellopsis* and *Zosime*, which now belong to Idyanthidae and Zosimidae respectively) were the most abundant of the 13 harpacticoid families (Shimanaga *et al.*, 2004).

At the family level, the copepod fauna of the coral degradation zone does not seem to differ markedly from other deep-sea studies on soft slope and abyssal sediments. Certain genera, such as *Bradya*, *Eurycletodes*, *Malacopsyllus*, *Marsteinia*, *Mesocletodes*, *Pseudomesochra* and *Zosime*, are typically found in any deep-sea study (Hicks and Coull, 1983; Seifried, 2004) and are also present in the Porcupine Seabight. While other families, genera and species do occur, detailed comparison at genus or even species level is restricted as no complete diversity analysis has been made of north-east Atlantic copepod communities (Vincx *et al.*, 1994). The study of deep-sea harpacticoids from the Great Meteor Seamount (which reaches about 270 m depth) by George and Schminke (2002) is at present the most closely situated study area, located west of the Canary Islands in the subtropical North Atlantic. George and Schminke (2002) detected 28 supraspecific taxa with Paramesochridae, Ectinosomatidae, Diosaccidae and Tisbidae as the most abundant. Of the 11 suprageneric taxa, which were analysed at species level, Argastidae was the most species-rich with seven genera and 40 species (in the Porcupine Seabight, this family consists of six genera and 18 species). Most of the suprageneric taxa from the Great Meteor Seamount were also present at the Porcupine Seabight, apart from Canuellidae, Cerviniidae, Cyliropsyllinae, Leptastacidae, Leptopontiidae and Styraethoracidae.

Harpacticoids exhibit an obvious and enormous variety of morphological forms as adaptations to special conditions in various marine habitats (Noodt, 1971). Body shape often reveals information regarding habitat type and it has been noticed that phytal associates generally possess a modified P1 which is strongly prehensile (Bell *et al.*, 1987). Certain taxa of the coral degradation zone have a morphology which appears typically epifaunal (such as in *Lobopleura*, *Peltobryda* (depressed); *Idyanthe*, *Idyella* (fusiform depressed); *Tegastes* (laterally compressed)) and

some of the identified species (*Klieosoma triarticulatum*, *Laophontodes mourois*, *Mesochra pygmaea*, *Laophonte elongata*) have even been reported from the washings of macroalgae (Lang, 1948; Hicks and Schriever, 1985; Arroyo *et al.*, 2003). So far, deep-sea tegastids have only been recorded from hard-substrate nutrient-rich environments (Gollner *et al.*, 2008). The occurrence of *Tegastes* in a coral sample again points to a preference of deep-sea tegastids for hard substrates. Furthermore, the occurrence of four ectinosomatid genera with prehensile first legs is exceptional in the deep sea and represents an indication of the specific nature of this habitat (Gheerardyn *et al.*, 2008a). It seems that the hard biogenic substrates of the coral degradation zone provide a suitable habitat for these epifaunal harpacticoids. However, knowledge of the harpacticoid fauna in the NE Atlantic is at present too limited to assess to what extent the taxonomic composition is modified by the presence of these complex, hard substrates compared to the surrounding soft-bottom deep sea.

Comparison with the harpacticoid fauna in a tropical reef lagoon

Composition

Comparison of the family composition of sediment and dead coral fragments in the tropical lagoon of Zanzibar and the deep sea of the Porcupine Seabight indicates that the two regions harbour different faunas. Families like Ameiridae, Argestidae, Ectinosomatidae, Miraciidae and Pseudotachidiidae are typically abundant in the soft-bottom deep sea, and are also important in the examined microhabitats of the cold-water coral degradation zone. Certain families with a preference for deep-sea habitats, e.g. Argestidae, Neobryidae, Pseudotachidiidae and Zosimidae (Seifried, 2004; George, 2004), were only found in the Porcupine Seabight and were absent in the tropical lagoon. The phytal families Dactylopusiidae and Tisbidae are very rare in the deep sea (Seifried, 2004) and were restricted to the tropical lagoon. Several families (Ameiridae, Ectinosomatidae, Miraciidae), are important in both regions, but these taxa are abundant in all marine habitats and are also generally important in all deep-sea studies. The difference in community structure between both regions is even more evident at the genus level, with only 18.8% of the total number of genera being shared. It is plausible that the extremely different en-

vironmental conditions and evolutionary histories of both geographically and bathymetrically separated ecosystems are responsible for this difference in community structure, despite the presence of comparable substrates.

The distinction between coral and sediment is more obvious in the tropical lagoon than in the cold-water coral degradation zone. The tropical coral fragments contained a specific assemblage composed of typical phytal taxa (such as Tisbidae and Dactylopusiidae) along with other eurytopic and sediment-dwelling forms (Gheerardyn *et al.*, 2008b). In the tropical lagoon, there is a large variety of habitat types (such as seagrasses, fossilised coral reef, seaweed farms), and these habitats might supply the phytal and epibenthic taxa which are present on the coral fragments. In the deep-sea environment, the number and occurrence of different substrate types (outside of the coral habitats) is much more limited. It is possible that most of the associated fauna is recruited from the surrounding soft sediments and this might explain the apparent lack of difference at the family level between sediment and coral substrates. This observation might also reflect differences in sampling between the two regions. In the cold-water coral degradation zone, the sediment could only be sampled from directly underneath the sampled coral fragments, while in the tropical lagoon the core was inserted in the sediment just next to the coral fragments.

Species diversity

Tropical coral reefs are known as the most taxonomically diverse of all marine ecosystems (Knowlton, 2001). Recently, it has been stated that the diversity of *Lophelia pertusa* cold-water coral reefs might be of a similar order of magnitude to that of some shallow-water coral reefs (Rogers, 1999). The present study aimed to compare species diversity of harpacticoid copepods associated with tropical and cold-water coral substrates. Although the large differences in sampling scale and effort (two sites 70 km apart along the Zanzibari coast versus six sites within a range of 2 km in the Porcupine Seabight) restrict comparisons, it seems that species richness and evenness of both microhabitats in the tropical lagoon are lower than in the deep sea. This would not be unexpected as the deep sea is known for its surprisingly high species diversity (Thistle, 1978; Seifried, 2004).

Reflections on the origin of the fauna

At the family level, the harpacticoid fauna of the cold-water coral degradation zone does not seem to differ strongly from deep-sea studies of soft-bottom communities. However, at present, it is difficult to assess to what extent the composition at the genus or species level in this specific habitat is different from the surrounding soft-bottom deep sea. Evidently, there is an urgent need for information on the harpacticoid assemblages of sediments outside the coral degradation zone, and of the European continental slopes more generally. Whether the high percentage of new species reflects the specificity of the harpacticoid community in this habitat has to be considered after more systematic investigations of neighbouring Atlantic regions. An important question to solve is what the affinities with other habitats are of the fauna found in *Lophelia pertusa* reefs.

We propose three hypotheses for the colonisation of this habitat:

(1) The majority of associated species are recruited from the background community and are thus present in the local geographical area. These species could be considered as facultative inhabitants of the coral degradation zone. As a consequence, regional diversity would not be increased substantially by the presence of these coral reefs. Nevertheless, the complex habitat-providing structures may increase abundance and species richness locally and therefore represent patches with high harpacticoid diversity. However, the presence of typically epifaunal taxa points to unique species associated with the coral substrates.

(2) Another possibility is that there is an exchange with shallow water areas. One piece of evidence that may support this is that some of the identified species show a large bathymetric distribution from the shallow subtidal (or even the littoral) to bathyal depths. Certain species have only been reported from shallow waters so far. This would indicate that an appropriate substrate (and related environmental conditions) is more important than water depth. *Lophelia pertusa* reefs occur along the European continental margin with their main depth distribution between 200 and 1000 m (Rogers, 1999). In Norway, these reefs occur in fjords where they may penetrate up to within 50 m of the surface (Rogers, 1999; Fosså *et al.*, 2002), forming a connection with shallow water habitats.

Furthermore, some of the identified species (e.g. *Idyanthe dilatata*, *Idyella major*, *Laophonte elongata*, *Lobopleura expansa*, *Zosime bergensis*) have even been reported from Norwegian fjords.

(3) Recently, De Mol *et al.* (2002, 2005) hypothesised that deep-water coral larvae may have been transported along the pathway of the Mediterranean Outflow Water (MOW) along the European continental margin from a southern source, potentially the Mediterranean Basin. Following this hypothesis, Raes *et al.* (2009) proposed that at least part of the nematofauna associated with *L. pertusa* fragments could follow the same trajectory as the larvae of this coral species, resulting in a co-occurrence of the coral and these nematodes. Accordingly, the source for colonisation would be somewhere in the Mediterranean Sea or near the MOW outflow point in the North Atlantic. In analogy herewith, for the harpacticoid copepod fauna the MOW might form a connection with the Mediterranean Sea, where several of the identified species have been recorded.

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